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European Journal of Phycology

DOI:
10.1111/jpy.13051

Published: 01/12/2020

Peer reviewed version

J. Phycol. *, ***–*** (2020)

DOI: 10.1111/jpy.13051-20-029

SUMMER AND WINTER MARINE HEATWAVES FAVOR AN INVASIVE OVER NATIVE SEAWEEDS[1]

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Marine heatwaves (MHWs) are emerging as forceful agents of ecosystem change and are increasing in frequency, duration, and intensity with climate change. During MHWs, physiological thresholds of native species may be exceeded while the performance of invasive species with warm affinities may be enhanced. As a consequence, MHWs could significantly alter an ecosystem's invasive dynamics, but such interactions are poorly understood. Following a 10-d acclimation period, we investigated the physiological resistance and resilience of an intertidal rock pool assemblage invaded by the seaweed *Sargassum muticum* to realistic 14-d marine heatwave scenarios (+1.5°C, +2.0°C, +3.5°C) followed by a 14-d recovery period. We conducted mesocosm experiments in both summer and winter to investigate temporal variability of MHWs. MHW treatments had clear negative impacts on native seaweeds (*Fucus serratus* and *Chondrus crispus*) while enhancing the performance of *S. muticum*. This pattern was consistent across season indicating that acclimation to cooler ambient temperatures results in winter MHWs having significant impacts on native species. As climate warming advances, this may ultimately lead to changes in competitive interactions and potentially exclusion of native species, while invasive species may proliferate and become more conspicuous within temperate rocky shore environments.

Key index words: **climate change; ecophysiology; global change ecology; photophysiology; *Sargassum muticum*; thermal thresholds; winter warm spells**

***Abbreviations*: MHW, marine heatwave; PAM, pulse amplitude modulated**

Ocean warming and the proliferation of invasive species are two of the greatest components of ecosystem change. Both processes play significant roles in determining levels of biodiversity and can seriously alter community structure and function (Hoegh-Guldberg and Bruno 2010, Wernberg et al. 2016, Vergés et al. 2016). While the majority of research has investigated the effects of ocean warming and invasive species independently, there is increasing evidence suggesting they can act synergistically to alter ecosystems in complex ways (Stachowicz et al. 2002, Sorte et al. 2010, Strayer 2010, Miranda et al. 2019). Thus, understanding the interactions between invasive species and ocean warming will be imperative in predicting future ecosystem responses to climate change.

The majority of research on ocean warming has focused on rising mean temperatures that are causing the gradual redistribution of species and facilitating invasions all around the world (Walther et al. 2009, Diez et al. 2012, Molinos et al. 2016). More recently, changes in extreme summer temperatures seen during heatwaves have also emerged as forceful agents for ecosystem change. Such events occur in the ocean as well as the atmosphere and marine heatwaves (MHWs) can have profound impacts at the ecosystem level (Smale et al. 2019). Studies investigating MHWs have overwhelmingly focussed on summer extremes, as it is here where species-wide tolerances are exceeded. However, periods of anomalously high temperatures, relative to climatic means, can occur at any time of the year (Hobday et al. 2016). This is important as acclimation to cooler ambient temperatures can reduce thermal tolerance, a phenomena observed across many groups (e.g., plants: Badger et al. 1982; seaweeds: Lüning 1984; fish: Bulger and Tremaine 1985; crustaceans: Layne et al. 1987; molluscs: Chapple et al. 1998; corals: Berkelmans and Willis 1999; insects: Hu and Appel 2004). Therefore, both summer and winter MHWs, which are increasing under climate change (Oliver et al. 2018) may

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Editorial Responsibility: T. Wernberg (Associate Editor)

still have implications for organism physiology, phenology, and competitive interactions.

At temperate latitudes, rocky reefs are dominated by macroalgae that play a fundamental role in providing habitat and maintaining the healthy function of the wider ecosystem (Teagle et al. 2017). The geographic distributions of macroalgae are largely constrained by temperature (Eggert 2012) and recent summer MHWs have caused changes in macroalgal primary productivity, community composition, and biogeography (Vergés et al. 2014, Wernberg et al. 2016, Straub et al. 2019, Thomsen et al. 2019). Seasonal acclimation is also commonplace in temperate macroalgae where it is used to maximize performance over a broad range of temperatures (e.g., Davison 1987, Dudgeon et al. 1990, Kübler and Davison 1993, Pfetzing et al. 2000, Padilla-Gamino and Carpenter 2007). This means that overall thermal tolerance may be lowered in winter and may also make macroalgae vulnerable to winter MHWs. However, while the effects of summer MHWs on macroalgae are increasingly recognized, the effects of winter MHWs remain relatively unexplored.

Successful invasive species often have much broader environmental tolerances than coexisting resident species (Dukes and Mooney 1999, Sorte et al. 2010). This means the extreme temperatures seen during MHWs may stress resident populations, while also making conditions more favorable for an invader (Diez et al. 2012). This may erode the resilience of a native species through decreased competitive performance and possible mortality while simultaneously increasing the invasibility of a nonnative through enhanced competitive performance and physiological condition. This is likely to be particularly beneficial to invaders currently in a lag phase or those that are established but unable to outcompete native species under ambient conditions.

Macroalgae represent a significant proportion of total marine invasives (20–30%; Schaffelke and Hewitt 2007, Thomsen et al. 2016) many of which proliferate following a summer MHW (Straub et al. 2019). *Sargassum muticum* is a high profile highly invasive canopy-forming seaweed (Norton 1977, Schaffelke et al. 2006, Andreakis and Schaffelke 2012). Native to Asia, it was introduced to North America in the 1940s and to Europe in the 1970s (Critchley et al. 1990) and has since established a cosmopolitan distribution (Engelen et al. 2015). Its wide thermal tolerance, high fecundity, and rapid growth mean it can quickly establish in new ecosystems (Norton 1977, Pedersen et al. 2005). Like most invasive species, there is a lag phase (period of slow population growth) before populations can start to outcompete native species. For *S. muticum*, this lag phase can be prolonged by the presence of functionally equivalent native species (Sanchez and Fernández 2005, Engelen and Santos 2009). However, once established it can rapidly accumulate biomass, outcompete native macroalgae in the acquisition of light and space resources, and change associated invertebrate community structure (Stæhr et al. 2000, Britton-Simmons 2004, Salvaterra et al. 2013). Therefore, understanding the future invasive dynamics of this species will be fundamental to future management of invaded systems.

The NE Atlantic has warmed significantly in recent decades (Belkin 2009, Smyth et al. 2009, Oliver et al. 2018), including increased frequency of periods of extreme marine weather (Scannell et al. 2016), a pattern that is set to accelerate in the future (IPCC 2018, Oliver et al. 2019). This may affect the invasive dynamics of *Sargassum muticum* and coexisting native species. Here we investigate the resistance (the ability to withstand elevated temperatures during MHW exposure) and resilience (the ability to recover from a MHW event) of a common rock pool assemblage (*Fucus serratus* and *Chondrus crispus*) invaded by *S. muticum* to realistic winter and summer MHW scenarios. In doing so we aim to understand i) how this community may look in the future ii) the seasonal effects of MHWs and iii) how MHWs may mediate invasion trajectories.

MATERIALS AND METHODS

Regional heatwave characteristics. MHW characteristics were calculated following the definition given by Hobday et al. (2016; see their table 2): here, a MHW is defined as an exceedance of the 90th percentile of the climatological seasonal temperature for at least 5 d. The sea surface temperature data used for our MHW characterization comes from the Copernicus Marine Environment Monitoring Service Iberia-Biscay-Ireland Regional Sea reanalysis/forecast datasets, which are downloadable from the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu/services-portfolio/access-to-products/). For the period 1992–2016 the IBI_REANALYSIS_PHYS_005_002 product and for the period 2016–2018 IBI_ANALYSIS_FORECAST_-PHYS_005_001 were used. The two datasets were combined to maximize the temporal cover of the temperature data. Daily means of the hourly mean temperature data were used for all calculations. The baseline period was set as 1993–2017 (this period was selected as no data was present before January 1st, 1992 and after December 31st, 2018 for the calculation of the 11 d running mean). The temperature climatology for each day of the year was calculated as the 11-d running mean (5-d either side of the given days) over the baseline period following Hobday et al. (2016). The 90th percentile of the temperature climatology was determined for each day using the same 11-d moving window over the baseline period.

Over the period 1992–2018, a total of 15 summer MHWs and 11 winter MHWs were identified. In summer, the average duration of a marine heat wave was 14.2 d with a mean temperature anomaly above the climatology of 1.9°C (±0.2 SD). The maximum temperature anomaly during a summer MHW was 3.4°C in 2018. For winter, a very similar mean duration of 13.4 d and mean temperature anomaly of 1.9°C (±0.2 SD) was found. The maximum temperature anomaly of 2.8°C during a winter MHW occurred in the winter of 2015/2016.

From these results, three perturbation levels were identified for the treatment of the seaweeds: +1.5°C (low intensity heatwave), +2.0°C (medium heatwave intensity) and +3.5°C (maximum heatwave intensity).

Macrophyte collection. Mature *Fucus serratus, Sargassum muticum* and *Chondrus crispus* individuals were haphazardly collected from low shore rock pools in January and June 2019 from College Rocks, Aberystwyth, UK (52°24′59.4″ N 4°05′26.1″ W). These were transported back to the laboratory in cool dark containers where they were cleaned from any epiphytes and placed in large communal tanks at ambient sea temperature (January: 9.0°C; June 14.0°C) overnight before being assigned to their experimental treatments.

Experimental design. Experiments were conducted in January and June to reflect both winter and summer MHW scenarios respectively. Both experiments used the same protocol, measurements and statistical analysis. The experimental setup consisted of four independent recirculatory seawater systems, representing a particular experimental heatwave scenario (ambient, +1.5, +2 and +3.5°C). Each system was filled with unfiltered seawater and consisted of five 35-L experimental aquaria connected to a 200-L reservoir with water recirculated in a closed loop. Each experimental aquaria received water from the reservoir at a flow rate of ~1.5 $L \cdot min^{-1}$ and was aerated with its own air stone. Each of these tanks had a single individual of each species within it. Individuals were left within treatment tanks to acclimate to experimental conditions at ambient sea temperature (January: 9.0°C; June 14.0°C) for 10 d, to ensure the experiment started from non-stressed conditions. Light was provided by cool white florescent tubes under a light regime reflective of the time of year of the experiment (January: 10:14 h L:D; June 16.5:7.5 h L:D). In the field, these species will experience a wide range of light intensities (up to full sunlight at low tide). We kept all individuals under a photosynthetic flux density of ~50 μmol photons $\cdot m^{-2} \cdot s^{-1}$, which is in excess of the light compensation point for intertidal seaweeds (~2 to 7 μmol photons $\cdot m^{-2} \cdot s^{-1}$; see Hurd et al. 2014). To ensure nutrients were not a limiting factor for growth or photosynthetic performance during the experiment, nitrates (NO_3), and phosphates (PO_4) were added to each system at a concentration of 100 μmol and 10 μmol respectively at the beginning of the acclimation period. Nutrient levels were checked weekly on an auto-analyzer to ensure they remained suitably elevated.

Rates of warming and cooling followed a "slow onset" MHW (Hobday et al. 2016), whereby the onset of warming at the beginning of the MHW is slower than the decline at the end. After the 10-d acclimation period, the temperature within each system was increased by 0.5°C per d until the experimental treatment had been achieved. Once experimental temperatures were achieved, treatments lasted 14 d, which represented the mean duration in the region. At the end of the heatwave treatment, temperatures were reduced at a rate of 1°C a d until control temperatures were reached and individuals were left to recover for 14 d (Fig. S1 in the Supporting Information). Temperature within each system was maintained using chillers (TECO SeaChill TR20, TECO, Ravenna, Italy) and measured along with salinity daily (TetraCon 325; WTW GmbH, Weilheim, Germany). Each treatment tank ran independently, which allowed different completion dates. This was necessary due to the varying length of time it took to reach different experimental (at the start of the MHW) and control temperatures (at the end of the MHW) for different MHW treatments.

Growth. Growth of each species was measured by recording the length from the holdfast to the end of the longest frond. Length of individuals was recorded prior to treatment exposure (day 0), after exposure to the MHW treatment (day 14), and after the recovery period (day 28). All measurements were taken to 0.01 cm with growth rate ($cm \cdot d^{-1}$) calculated for all individuals as length increase (cm)/period of treatment exposure (d).

Photosynthetic performance. Photosynthetic performance was determined using Pulse Amplitude Modulated (PAM) fluorometery (Diving-PAM; Walz, Effeltrich, Germany). Specifically, we used the maximum quantum yield of photosystem II (PSII) as a rapid integrative measure of photosynthetic performance. PAM fluorometry measures a maximum value of chlorophyll *a* fluorescence (F_m) during exposure to a rapid saturation pulse of light while all reaction center are closed. Using this information and the minimal level of fluorescence when all reaction centers are open (F_o) it is possible to calculate the variable fluorescence ($F_v = F_m - F_o$). Theoretical and empirical studies have shown the ratio of variable florescence to maximal fluorescence (F_v/F_m) to be a robust indicator when calculating the maximum efficiency of PSII activity (Butler 1978, Genty et al. 1992) and is commonly used to assess thermal stress in seaweeds (e.g., King et al. 2018). A reduction in F_v/F_m occurs under stressful conditions which result in photoinhibition or inactivation damage to PS II (Murchie and Lawson 2013). Fronds were dark-adapted using dark-acclimation leaf clips for 15 min before each measurement. F_v/F_m measurements were taken out of water at the same time in the morning, every 3 days, from the uppermost part of the thallus of each individual ($n = 5$ per treatment).

Statistical analysis. Both growth and photosynthetic performance were analyzed using Repeated Measures Analysis of Variance (RM ANOVA) in IBM SPSS Statistics v.24. (IBM Corp, Armonk, NY, USA). Each model had three factors: species (three levels: *Chondrus crispus*, *Fucus serratus*, and *Sargassum muticum*), temperature (four levels: Control, +1.5°C, +2.0°C, +3.5°C), and time (three levels: pre-MHW, MHW, recovery). To ensure equal variances between all combinations of all levels, a Mauchly's test for Sphericity was performed. Where assumptions of Sphericity were violated, degrees of freedom were corrected using the Greenhouse–Geisser value as an estimate of Sphericity. Significant differences ($P < 0.05$) were further investigated using pair-wise comparison LSD post hoc tests. All values presented as means ± standard error (SE).

Winter and summer heatwave experiments were treated independently as by necessity the experiments were run at different times. Consequently, only qualitative comparisons are drawn from the two experiments.

RESULTS

Growth. Growth rates varied significantly between species, temperature and time during the winter and summer MHW experiments (Tables S1–S8 in the Supporting Information). For *Chondrus crispus,* summer and winter MHWs had a similar effect on growth rates. In both seasons, there was no difference in growth rate across MHW treatments or between the MHW and recovery period (Fig. 1, a and b; Tables S3–S6). However, in both seasons there was a non-significant trend whereby growth was reduced in all MHW treatments compared to the control. *Fucus serratus* showed different responses to MHWs depending on the season in which the study was undertaken. In winter, *F. serratus* growth was not affected by the +1.5°C or 2.0°C MHW treatments. However, by the end of the +3.5°C MHW, growth was significantly greater than

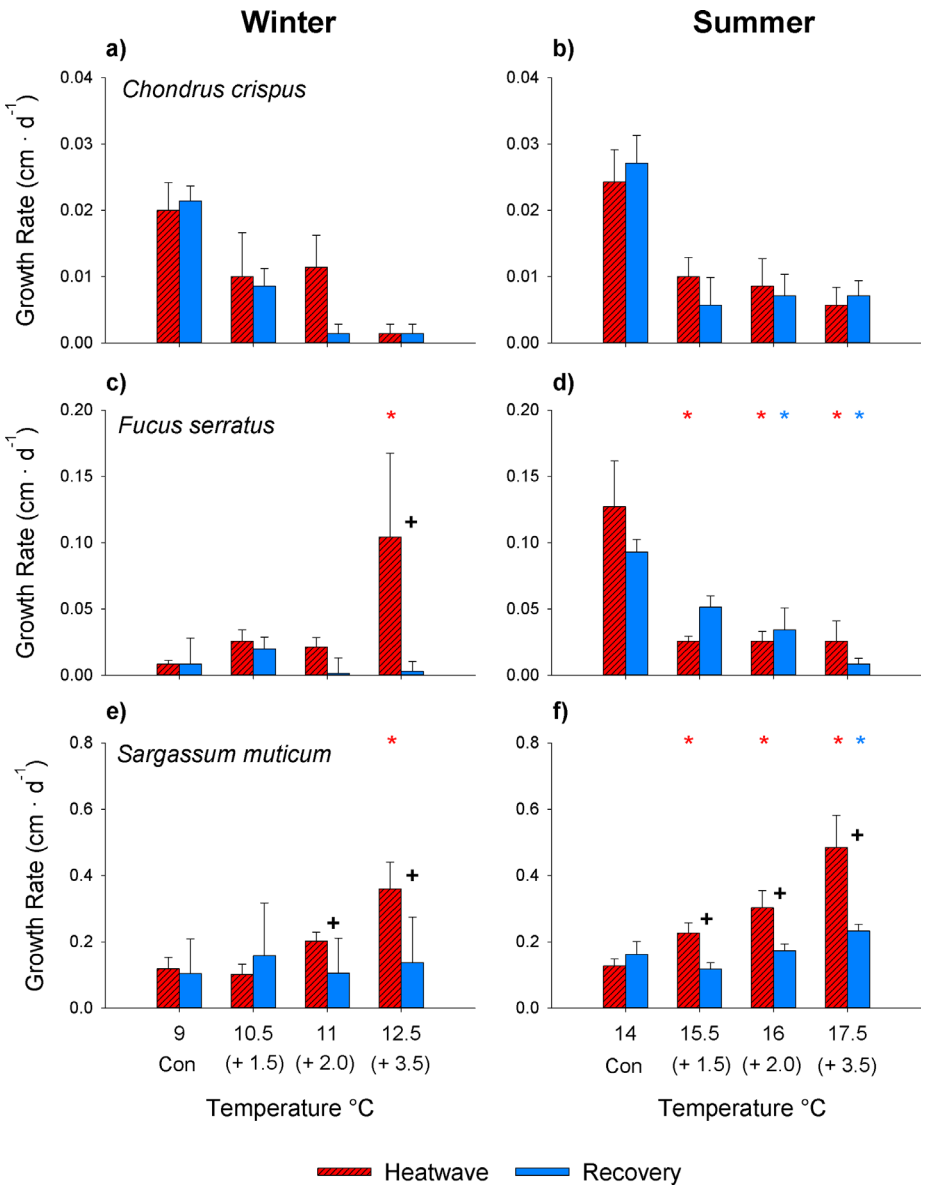

FIG. 1. Mean (+SE) growth rate (cm · d^{-1}) for *Chondrus crispus* (a + b), *Fucus serratus* (c + d), and *Sargassum muticum* (e + f) to winter (left) and summer (right) in response to marine heatwave mesocosm experiment. * indicates significant difference from control values. + indicates significant difference between end of MHW and recovery periods.

control values (Fig. 1c; Table S3; LSD post hoc, $P = 0.049$). This elevated growth rate was not observed in the subsequent recovery period where values were significantly reduced and similar to the control levels (Tables S3 and S4). In summer, *F. serratus* growth rates were significantly lower than control values at the end of all the MHW treatments (Fig. 1d, Table S5; LSD post hoc, $P = 0.048$ for all treatments). During the recovery period, growth rates returned to control values in the +1.5°C treatment, but remained significantly depressed in the +2.0°C (LSD post hoc, $P = 0.015$) and 3.5°C (LSD post hoc, $P = 0.001$) treatments (Fig. 1d; Tables S5 and S6). As with *C. crispus*, growth of *Sargassum muticum* followed similar patterns across the two seasons. In general, elevated growth was apparent by the end of MHW treatments and increased with increasing MHW intensity (Fig. 1, e and f). This pattern was most marked in summer where growth was significantly greater than control values at the end of all MHW treatments (Table S5; LSD post hoc, +1.5°C, $P = 0.05$; +2.0°C, $P = 0.001$; +3.5°C, $P < 0.001$), whereas this occurred only in the +3.5°C treatment in winter (Table S3; LSD post hoc, $P < 0.001$). Elevated growth seen at the end of MHWs was not observed during recovery periods. Here, growth rates were comparable to control values except in the +3.5°C summer MHW treatment where growth remained elevated (Table S5, LSD post hoc, $P = 0.003$).

Photosynthetic performance. Photosynthetic performance varied significantly between species, temperature and time during the winter and summer MHW experiment (Tables S9–S16 in the Supporting

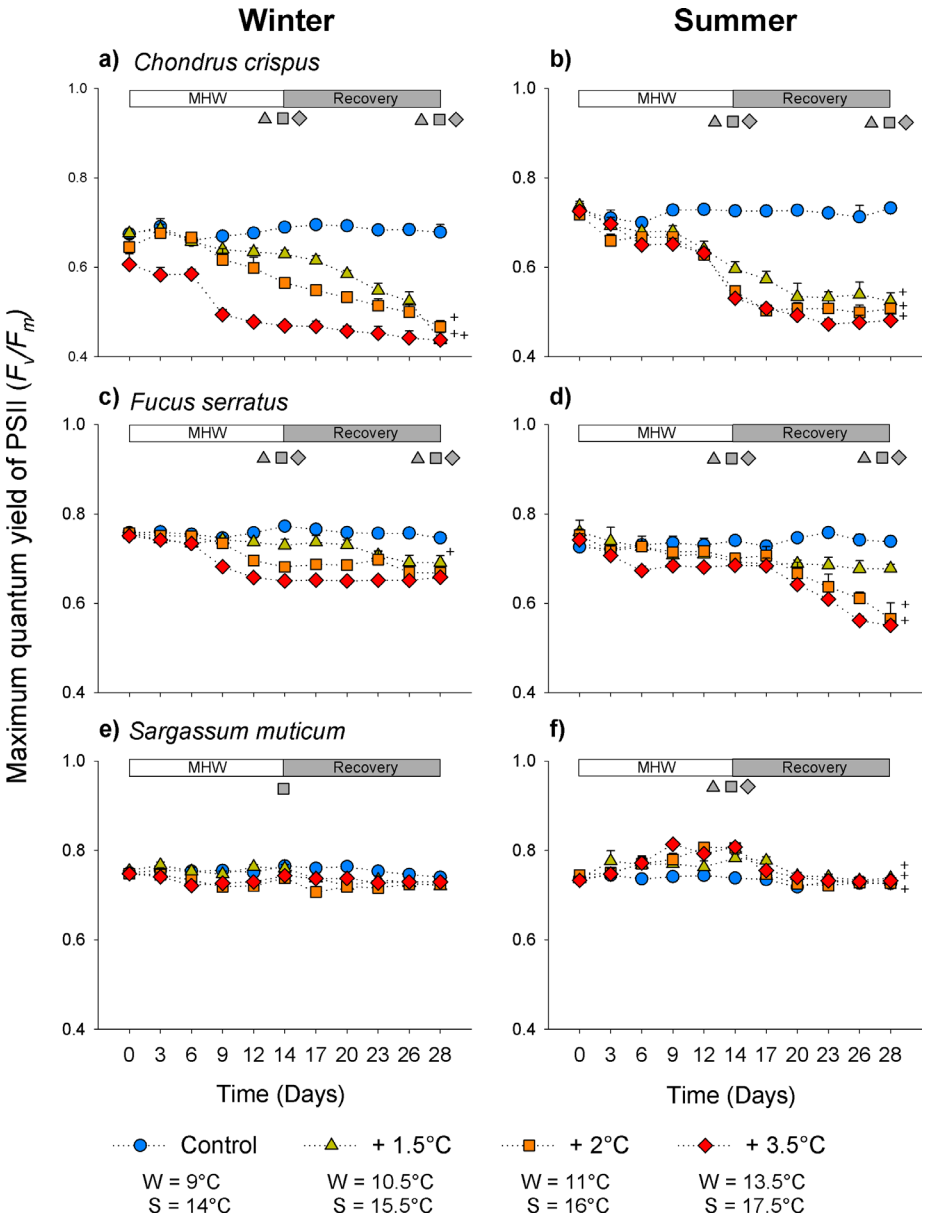

FIG. 2. Mean + (1 SE) F_v/F_m values for *Chondrus crispus* (a + b), *Fucus serratus* (c + d), and *Sargassum muticum* (e + f) to winter (left) and summer (right) in response to marine heatwave mesocosm experiment. Gray symbols indicate significant difference from control values. + indicates significant difference between end of MHW and recovery periods. Formal analysis based on sampling at the end of MHW and recovery periods.

Information). Both summer and winter MHW treatments had similar effects on the photosynthetic performance of *Chondrus crispus*. F_v/F_m values were significantly lower than control values following all MHW intensity treatments, in both winter (Fig. 2a; Table S11; LSD post hoc, $P < 0.001$ for all treatments) and summer (Fig. 2c; Table S12; LSD post hoc, $P < 0.001$ for all treatments). These values continued to decline and by the end of the recovery period were significantly lower than at the end of the MHW treatments for both winter (Fig. 2a; Table S13; LSD post hoc, +1.5°C, $P < 0.001$; +2.0°C, $P < 0.001$; +3.5°C, $P = 0.027$) and summer experiments (Fig. 2c; Table S14; LSD post hoc, +1.5°C, $P < 0.001$; +2.0°C, $P = 0.047$; +3.5°C, $P < 0.001$). Similarly, photosynthetic performance of *Fucus serratus* followed a similar pattern across the two seasons with F_v/F_m values significantly lower than control values following all MHW intensity treatments in both winter (Fig. 2b; Table S11; LSD post hoc, $P < 0.001$ for all treatments) and summer (Fig. 2d; Table S12; LSD post hoc, +1.5°C, $P = 0.022$; +2.0°C, $P = 0.048$; +3.5°C, $P = 0.007$). In winter, by the end of the recovery period, F_v/F_m values were similar amongst treatments, still significantly lower than control values (Fig. 2d; Table S11; LSD post hoc, $P < 0.001$ for all treatments) but had not declined significantly compared to the end of the MHW (Table S13). In summer, F_v/F_m values continued to fall throughout the recovery period for the +2.0°C and +3.5°C treatments. By the end of the summer recovery period, F_v/F_m values in these treatments were significantly lower than at the end of the MHW (Table S14; +2.0°C and +3.5°C, LSD post

hoc, $P < 0.001$). In contrast to the native species, winter MHW treatments had little effect on the photosynthetic performance of *Sargassum muticum* (Table S11). In summer, F_v/F_m values were significantly elevated at the end of all MHW treatments (Fig. 2f; Table S12; LSD post hoc, +1.5°C, $P = 0.031$; +2.0°C, $P = 0.001$; +3.5°C, $P < 0.001$) but returned to control values by the end of the recovery period.

DISCUSSION

Here we have shown a clear difference in the ability of two native and one invasive seaweed to tolerate and recover from realistic summer and winter MHW scenarios. Specifically, *Sargassum muticum*, one of the most high profile and prolific invasive seaweeds, demonstrated elevated growth during almost all MHW scenarios. Moreover, F_v/F_m values indicated winter MHWs were not stressful while by the end of the summer MHW F_v/F_m values were elevated compared to controls. Conversely, our two native seaweeds were generally negatively impacted by MHW scenarios. For *Chondrus crispus,* growth was up to three times less in experimental treatments, and both species demonstrated a decline in F_v/F_m values after MHW exposures and did not recover during the recovery period. In many cases they continued to decline. This indicates that these individuals suffered from irreversible or partly irreversible stress. While these effects were nonlethal, at the point the experiment was terminated, they may have wider implications on the future invasion dynamics of the system. Moreover, the results demonstrate that both summer and winter MHWs may can have more subtle effects on macroalgae beyond that of mortalities due to exceedance of the species' thermal tolerance levels.

Summer MHWs have caused widespread mortalities and acute stepwise range contractions in seaweed populations at their trailing edges, as species-wide thermal tolerances are exceeded (e.g., Wernberg et al. 2013). Our study site is within the center of our native species' range whose trailing edges are located at the Cantabrian Sea along Spain's northern coast. Here summer seawater temperatures reach >20°C, and as such, it is not surprising we did not observe mortalities, as even our most extreme summer MHW (17.5°C) scenario is within the thermal window of both species. Similar research at the range center of *Chondrus crispus* and *Fucus serratus* has shown individuals can survive 1 week exposures of up to 25°C (Lüning 1984). However, despite no lethal effects, photophysiology showed our summer MHW treatments were still stressful to these native species. Examples from other range center seaweed populations are rare but similar sublethal effects of simulated summer MHWs have been observed from range center populations of the sugar kelp, *Saccharina latissima*, in Denmark (Nepper-Davidsen et al. 2019). The wider implications of such nonlethal stress is unknown but it can have long lasting effects on performance, through the reallocation of resources, or may reduce resilience to other stressors. For example, wide spread population loss of the bull kelp, *Durvillaea* spp., was observed in range center populations in New Zealand, when a summer MHW coincided with unusually high air temperatures (Thomsen et al. 2019).

Research on MHWs has largely focused on summer extremes and winter impacts are for the most part unknown. F_v/F_m values indicated that none of our study species were stressed by summer control treatments (14°C) but temperatures below this were stressful during our winter MHW (10.5–13.5°C) for the native species. In many cases, similar relative increases in temperature (+1.5, 2, and 3.5°C) caused similar declines in F_v/F_m values in both summer and winter MHWs. This indicates thermal tolerances have been considerably lowered in native species making winter MHW treatments stressful. While *Fucus serratus* and *Chondrus crispus* will experience and recover from higher temperatures than our MHW treatments over a tidal cycle, it seems persistent smaller temperature increases impair cellular processes and outpace the wider acclimation capacity of both species. Seasonal acclimation is commonplace in temperate macroalgae, particularly in intertidal species where it can increase resistance to the shifting seasonal low tide extremes (e.g., Davison 1987, Kübler and Davison 1993, Eggert et al. 2003). Therefore, winter MHWs may also cause stress in other temperate species and study systems.

Seaweed growth is often seasonally controlled and can be regulated by changes in temperature and nutrients (e.g., Kain 1987). Therefore, MHWs have the potential to disrupt seasonal growth phenology by exceeding threshold temperatures and triggering growth. In our study, growth rates in both *Chondrus crispus* and *Sargassum muticum* were similar between summer and winter control treatments, indicating little effect of seasonal temperature on their growth patterns. For *Fucus serratus,* which displays a clear summer growth season (e.g., Keser and Larson 1984), growth was depressed in winter control treatments and considerably greater in summer. However, in our highest intensity winter treatment (12.5°C/+3.5°C), growth rates approached that of summer controls, before plummeting again during the recovery period. Here, it is likely elevated temperature, either alone or in combination with elevated nutrients, has triggered growth in *F. serratus,* despite photophysiology showing this to be a stressful treatment. It is likely this growth was mediated through the mobilization of storage sugars (Kremer 1981) but the underlying mechanism remains unresolved. Nonetheless, the potential for seasonal uncoupling of growth phenologies deserves further attention.

MHWs are set to become even more frequent, intense and last longer under future climate change scenarios (Oliver et al. 2019). This means that the heatwave scenarios here will likely become the new norm over the coming decades (Stillman 2019). Therefore, in the near future, *Sargassum muticum* is likely to regularly benefit from MHWs at the detriment of native species, which will regularly be experiencing sublethal stress. This may result in natives becoming competitively excluded by *S. muticum*, which will be able to more readily proliferate. For example, increased growth demonstrated by *S. mutcium* could result in spatial exclusion, shading, or displacement of competitors from substrate (e.g., Stæhr et al. 2000). Such interspecific differences in sublethal stress have long been known to result in different vertical distributions on rocky shores. For example, zonation of intertidal fucoids is predominantly driven by a species' ability to better tolerate sublethal stress (e.g., Hartnoll and Hawkins 1985, Chapman and Johnson 1990). As such, as ocean warming progresses, *S. muticum* may become a much more conspicuous member of the NE Atlantic rocky shore community. This may be particularly true where *S. muticum* coexists with species at their trailing edges where MHWs will be most stressful for native species and where the majority of native population declines occur (Smale et al. 2019).

Here we used growth and photophysiology to increase our understanding of how extreme summer and winter temperatures will affect the future invasive dynamics of a temperate intertidal system. The extent to which ocean warming will influence ecosystem change requires more attention and it is increasingly recognized that physiology can be used to develop evidence-based climate change policies (Stillman 2019). However, further work is required to fully understand what our results mean at the ecosystem level. For example, it is not known whether proliferation of *Sargassum muticum* will change ecosystem function or whether it will act functionally similar to other canopy-forming species that it may replace. Such knowledge will be fundamental in driving any future management intervention or policy change.

Funding was made available to support this research from the Institute of Biological, Environmental and Rural Sciences, Aberystwyth University. NGK and SBW were supported by the European Regional Development fund through Ireland Wales Cooperation Programme, BLUEFISH. Additional thanks to Rory Geoghegan and Maisy Gee for assistance with collecting the data. We thank three anonymous reviewers for their thoughtful reviews, which have significantly improved the manuscript.

AUTHOR CONTRIBUTIONS

JA: conceptualization-lead, data curation-lead, formal analysis-lead, investigation-lead, methodology-equal, writing-original draft-equal, writing-review & editing-equal. NK: formal analysis-equal, supervision-equal, visualization-equal, writing-original draft-lead, writing-review & editing-lead. SW: data curation-equal, formal analysis-equal, methodology-equal. PM: conceptualization-lead, formal analysis-equal, funding acquisition-lead, methodology-equal, supervision-lead, visualization-equal, writing-original draft-equal, writing-review & editing-equal.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Graphical representation of experimental approach used to examine the effect of summer and winter marine heatwaves on *Fucus serratus*, *Chondrus crispus*, and *Sargassum muticum*. Experiments involved 10 d of acclimatization to seasonally adjusted ambient sea temperatures, followed by 14 d of heatwave simulation and a 14 d recovery period.

Table S1. Results of a repeated measures ANOVA to test for differences in the winter growth rate ($cm \cdot d^{-1}$) of *Chondrus crispus*, *Fucus serratus*, and *Sargassum muticum* in response to a 14 d MHW exposure (9.0, 10.5, 11.0, and 12.5°C) followed by a 14 d recovery period at ambient temperature (9.0°C). The model has three factors: Time, Species, and Temperature. Significant values ($P < 0.05$) are highlighted in bold.

Table S2. Results of a repeated measures ANOVA to test for differences in the summer growth rate ($cm \cdot d^{-1}$) of *Chondrus crispus*, *Fucus serratus,* and *Sargassum muticum* in response to a 14 d MHW exposure (14.0, 15.5, 16.0, and 17.5°C) followed by a 14 d recovery period at ambient temperature (14.0°C). The model has three factors: Time, Species, and Temperature. Significant values ($P < 0.05$) are highlighted in bold.

Table S3. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S1) for growth rates in the winter marine heatwave experiment. Comparisons are between temperatures for each species at specific time points.

Table S4. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S1) for growth rates in the winter marine heatwave experiment. Comparisons are between time points for each species and temperature.

Table S5. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S2) for growth rates in the summer marine heatwave experiment. Comparisons are between temperatures for each species at specific time points.

Table S6. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S2) for growth rates in the summer marine heatwave experiment. Comparisons are between time points for each species and temperature.

Table S7. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S1) for growth rates in the winter marine heatwave experiment. Comparisons are between species at each time point and temperature.

Table S8. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S2) for growth rates in the summer marine heatwave experiment. Comparisons are between species at each time point and temperature.

Table S9. Results of a repeated measures ANOVA to test for differences in the normalized winter F_v/F_m values of *Chondrus crispus*, *Fucus serratus,* and *Sargassum muticum* in response to a 14 d MHW exposure (9.0, 10.5, 11.0, and 12.5°C) followed by a 14 d recovery period at ambient temperature (9.0°C). The model has three factors: Time, Species, and Temperature. Significant values ($P < 0.05$) are highlighted in bold.

Table S10. Results of a repeated measures ANOVA to test for differences in the normalized summer F_v/F_m values of *Chondrus crispus*, *Fucus serratus,* and *Sargassum muticum* in response to a 14 d MHW exposure (14.0, 15.5, 16.0, and 17.5°C) followed by a 14 d recovery period at ambient temperature (14.0°C). The model has three factors: Time, Species, and Temperature. Significant values ($P < 0.05$) are highlighted in bold.

Table S11. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S9) for F_v/F_m values in the winter marine heatwave experiment. Comparisons are between temperatures for each species at specific time points.

Table S12. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S10) for F_v/F_m values in the summer marine heatwave experiment. Comparisons are between temperatures for each species at specific time points.

Table S13. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S9) for F_v/F_m values in the winter marine heatwave experiment. Comparisons are between time points for each species and temperature.

Table S14. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S10) for F_v/F_m values in the summer marine heatwave experiment. Comparisons are between time points for each species and temperature.

Table S15. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S9) for F_v/F_m values in the winter marine heatwave experiment. Comparisons are between species at each time point and temperature.

Table S16. Repeated measure ANOVA post hoc comparisons for Time*Species*Temperature interaction (Table S10) for F_v/F_m values in the summer marine heatwave experiment. Comparisons are between species at each time point and temperature.